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A CLASSIFICATION OF PLANTS INTO HIGHER TAXA BASED ON CYTOLOGICAL AND BIOCHEMICAL CRITERIA*

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Summary

A variety of schemes are employed currently for the classification of plants into higher taxa. The two most widely used schemes, the traditional kingdom Plantae with subkingdoms Thallophyta and Embryophyta, and the Whittaker five-kingdom system with plants in the kingdoms Monera, Protista, Fungi and Plantae, rely on nineteenth century morphological criteria for delimitation of taxa that result in polyphyletic assemblages of organisms. It is proposed that plants be assigned to seven kingdoms, subordinate to the superkingdoms Procaryota and Eucaryota which are based on the procaryotic and eucaryotic types of cellular organization. The distribution of accessory chlorophylls is used as a major taxonomic criterion for classifying photosynthetic organisms at the kingdom level. This results in a single kingdom, the Cyanochlorobionta for photosynthetic plants containing chlorophyll *a* only within the superkingdom Procaryota. Photosynthetic plants within the superkingdom Eucaryota have been divided into three groups, the kingdom Erythrobionta for organisms with no accessory chlorophyll or occasionally chlorophyll *d* (and lacking flagella), the kingdom Chlorobionta for organisms with accessory chlorophyll *b*, and the Ochrobionta for those organisms with accessory chlorophyll *c*. Vascular plants have been assigned to a single division, the Tracheophyta, since in addition to having a similar biochemistry (chlorophylls *a* and *b*, similar carotenoids, starch as a reserve food product) they possess also a basic morphological groundplan – a vascular system containing xylem and phloem, and a life history consisting of an alternation of generations. The fungi have been assigned three kingdoms as opposed to most extant schemes of classification in which they are allocated to a single polyphyletic assemblage. The true fungi have been divided into kingdoms Fungi 1 and Fungi 2 since it is thought that they have evolved from the Chlorobionta and Ochrobionta, respectively; the myxomycetes have been placed in a third kingdom, the Myxobionta.

A perusal of eighteen botanical books published in the U.S.A. during the last decade has revealed a considerable lack of uniformity in the usage of the higher categories of classification: five used the traditional two kingdom system of organisms with the kingdom Plantae for plants and the subkingdoms Thallophyta and Embryophyta; three employed the recently proposed five kingdom organismic system of Whittaker (1969) with plants in the kingdoms Monera, Protista, Plantae and Fungi; six began their treatment at the division level, presumably due to lack of satisfaction with existing schemes; and two proposed new systems for the subdivision of the traditional kingdom Plantae, Bold (1973), who has been followed subsequently by two authors, established the subkingdoms Prokaryonta, Chloronta, and Achloronta, and Neushul (1974) the subkingdoms Prokaryonta and Eukaryonta. In the last few decades a tremendous accumulation of cytological and biochemical data has occurred (Klein and Cronquist, 1967), but these have not been adequately utilized in classification. With the recent publication of compendia

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of ultrastructural (Dodge 1973) and biochemical data on algae (Stewart 1974), the time is opportune for a reassessment of the higher categories of classification of plants.

The division of organisms into plant and animal kingdoms has been a part of formal classification since the time of Linnaeus. The kingdom Plantae is divided into two subkingdoms, the Thallophyta and the Embryophyta (Thallobionta and Embryobionta in Cronquist, 1960 and Cronquist, Takhtajan and Zimmermann, 1966). The term Thallophyta was first used by Endlicher in 1836 as a kingdom (Smith, 1950), but was relegated to the status of a subkingdom by Tippo (1942) when he introduced the above two subkingdoms as widely used today. The two may be differentiated on the basis of the sex organs which in the Thallophyta are one celled, or if multicelled then all the cells are fertile, whereas in the Embryophyta the multicellular sex organs always have a layer of sterile outer cells. They may also be distinguished on the basis of the embryo since in the Thallophyta, except for the red algae, the embryo never develops into a multicellular embryo while still within the female sex organ. This system of classification, based on morphology, does not reflect evolutionary relationships adequately (Smith, 1951) and it is remarkable that it is so widespread in use today. The Thallophyta includes the algae and fungi, both of which are polyphyletic assemblages of organisms. Furthermore, this division of the plant kingdom separates the green algae from the higher plants in spite of the fact that the possession of similar biochemical criteria such as pigments and food storage products indicates their common evolutionary history (Smith, 1951; Strain, 1951; Lewin, 1974).

A second scheme of classification that is gaining acceptance is the five-kingdom organismic system of Whittaker (1969). Whittaker (1959) devised initially a four-kingdom system with the procaryotic organisms included in the Protista, but later followed Grant (1963) who split off the procaryotes to establish a five-kingdom system. The system is based upon two major premises: level of organization and type of nutrition. Three levels of organization are recognized – the procaryotic (kingdom Monera), eucaryotic unicellular (kingdom Protista), and eucaryotic multicellular and multinucleate. The three major types of nutrition that occur in organisms: photosynthesis by autotrophic plants, absorption by fungi, and ingestion by animals (Rogers, 1948) are used also to delimit kingdoms. Although the kingdom Monera has photosynthetic and absorptive nutrition, and the kingdom Protista photosynthetic, absorptive and ingestive nutrition, the delimitation of kingdoms at the multicellular and multinucleate level is based on nutritive modes – kingdom Plantae (photosynthetic), kingdom Fungi (absorptive) and kingdom Animalia (ingestive). Although Whittaker (1969) stated that the "evolutionary unity of common descent should underlie the coherence of taxa" he resuscitated a nineteenth century morphological concept, the Protista, that results in the splitting of several evolutionary lines. The straddling by certain algal divisions of the line between the unicellular and multicellular – multinucleate condition is a serious practical limitation e.g., the Phaeophyta are Plantae exclusively and the Cryptophyta and Euglenophyta comprise only Protista, but Chrysophyta, Chlorophyta, Rhodophyta and Pyrrhophyta contain organisms from both kingdoms. Whittaker acknowledges this difficulty but assigns the Chlorophyta and the Rhodophyta to the Plantae and the Chrysophyta and the Pyrrhophyta to the Protista. However these "stop-gap" measures serve to emphasize the fallability of his system and emphasize that the morphological criterion of unicellular versus multicellular – multinucleate has no profound evolutionary significance and cannot be used to delimit groups of organisms of common evolutionary descent.

The predominance today of multicellular plants and animals has led to a long standing and rigid view as to what constitutes plant and animal modes of nutrition. Many lower organisms, particularly unicellular phytoflagellates, do not fall conveniently into the nutritional categories outlined above. Because of the difficulty in the allocation of those organisms which are held to have intergrading plant and animal characteristics, attempts have been made from the nineteenth century to the present to create a third kingdom, variously called the Protista or

Protoctista (reviews by Copeland, 1938, 1947; Whittaker, 1959, 1969; Cronquist, 1960). This simplified viewpoint has hindered the creation of a phylogenetic classificatory system since the major categories of nutrition do not occur in mutually exclusive groups of organisms of common evolutionary descent. Phytoflagellates that lack photosynthetic pigments and thus need organic carbon occur in most algal divisions, although many are facultative heterotrophs and utilize organic carbon whilst retaining a photosynthetic potential. Furthermore, many obligately photosynthetic algae, in contrast to higher plants, require vitamins and are thus not strictly autotrophic (Provasoli and Carlucci, 1974). Colorless algae may be distinguished from colored ones solely on the absence of plastids; they otherwise possess an identical cellular morphology and ultratructure. The loss of plastids appears to have occurred as an abrupt change many times in nature and has been induced experimentally in these and in other algae (Leedale, 1967; Droop, 1974). Phagotrophy occurs also in three algal divisions, the Euglenophyta, Pyrrhophyta and Chrysophyta (Hutner and Provasoli, 1955), and there is also circumstantial evidence for the Cryptophyta (Shuster, 1968). Complex nutritional modes are not restricted to the algae but occur in flowering plants: insectivorous bog plants augment their nitrogen supply by trapping and digesting insects. All autotrophic eucaryotic organisms and related holozoic and phagotrophic forms should be considered as plants. That this is both feasible and practicable is indicated by the treatment of these organisms by zoologists (Honigberg et al., 1964); the phytoflagellates together with their colorless relatives are placed in a separate taxon (superclass Mastigophora, class Phytamastigophorea with the algal divisions as recognized by botanists given the status of orders) away from the truly animal Protozoa.

A third system, based also on morphological criteria is that of Copeland (1938, 1947, 1956) which Whittaker purports to improve; it is a four-kingdom system with Monera for procaryotes, Protoctista for organisms that lack the degree of tissue differentiation of higher plants and animals, and the Metaphyta and Metazoa for the higher plants and animals, respectively. Copeland includes the Chloropyta with the Metaphyta since they are part of the evolutionary line leading to the higher plants although the former lack marked tissue differentiation. Hutchinson (1967) employed a slightly modified scheme in which all algal divisions were assigned to the Protoctista. The kingdom Protoctista, regardless of which of the above two modifications is utilized, consists of a heterogeneous polyphyletic group since it includes the algae, fungi and Protozoa. Furthermore, it cannot be adequately circumscribed on the basis of the absence of marked tissue differentiation; the Phaeophyta contains certain organisms which have differentiation into holdfast, stipe and blade regions with a central vascular tissue containing sieve cells through which translocation occurs (Nicholson and Briggs, 1972); the fungi have limited somatic tissue differentiation but many have elaborate reproductive organs; the Bryophyta are included in the Metaphyta despite little tissue differentiation. The Copeland system clearly suffers from problems similar to the Whittaker scheme. The latter author was certainly not convinced of the advantages of his scheme over that of Copeland since he wrote "the practical difficulties with borderline groups are at least as great, and may be greater, when the separation is based on the unicellular condition rather than degree of tissue differentiation." As Cronquist (1960) pointed out, the multiple kingdom systems do not avoid the necessity of drawing arbitrary lines and create more arbitrary boundaries than existed previously.

Margulis (1971, 1974) has recently championed a modified version of the Whittaker scheme in which she accepts his basic tenets but has restricted the Fungi and Plant kingdoms. All flagellated and amoebiod organisms have been excluded from the Fungi which now contains only the Zygomycota, Ascomycota and Basidiomycota, together with the imperfect fungi and the lichens. The Chlorophyta, Phaeophyta and Rhodophyta have been removed from the kingdom Plantae, which now includes only the Bryophyta and the Tracheophyta. This has increased the monophyly of the Fungi and Plantae but it has created an even

Figures. – Plants have been assigned to seven kingdoms within the superkingdoms Procaryota and Eucaryota. Bacteria and animals have been tentatively assigned to separate kingdoms for convenience only since they were not considered in detail. The position that divisions have been placed in within each kingdom represents their degree of evolutionary change from the ancestral condition e.g., the Basidiomycota, Tracheophyta, and Phaeophyta are on the same level and represent the present-day culmination of evolutionary development within their respective higher taxa.

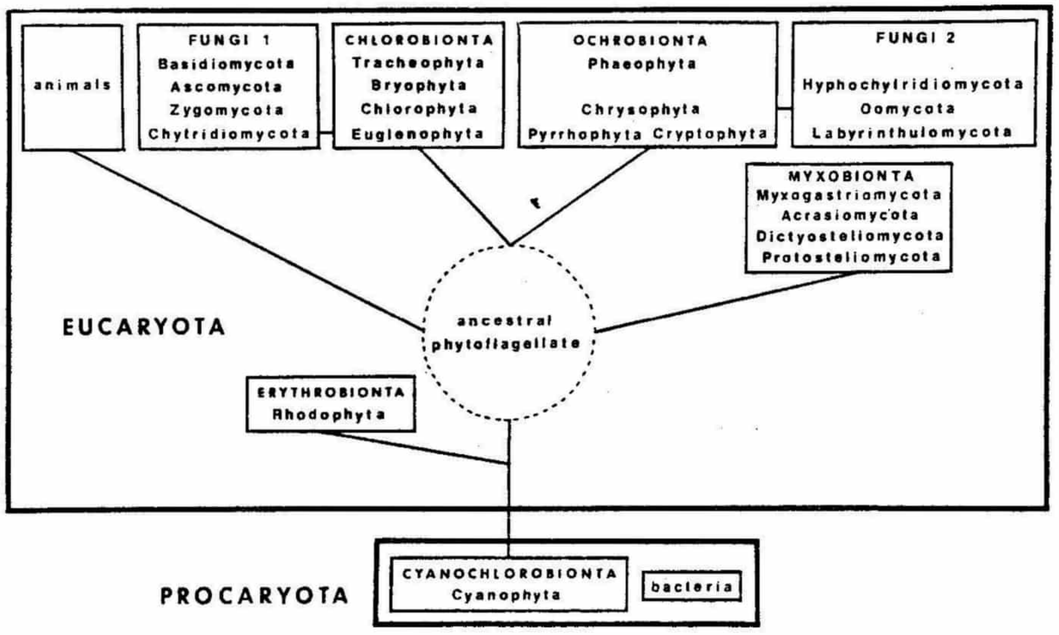

Fig. 1. The classical hypothesis for the origin of the eucaryotic cell by gradual evolutionary change from photosynthetic procaryotes containing chlorophyll *a*.

more heterogeneous and polyphyletic kingdom Protista. Margulis clearly recognizes the heterogeneity of the Protista since she refers to it as a "miscellaneous group of phyla in which profound evolutionary experimentation occurred" (Margulis, 1974). However, her rejection of the criterion of monophyly for the delimitation of kingdoms will preclude general acceptance of her scheme (Jeffrey, 1971; Leedale, 1974) since one of the most widely accepted aims of modern taxonomy is to provide a classification which expresses the natural or phylogenetic relationships of organisms (Davis and Heywood, 1963; Cronquist, 1968; Radford et al., 1974).

The living world clearly cannot be neatly divided into a small number of monophyletic kingdoms because of the tremendous diversity of organisms. The major taxonomic objective of establishing monophyletic assemblages of organisms should not be compromised for the sake of convenience as has occurred with the kingdoms Protista and Protoctista in the Whittaker and Copeland schemes, respectively. Jeffrey (1971) and Leedale (1974) have both proposed multiple kingdom systems based on a more valid taxonomic basis; the former divided the plant world into five and the latter into twelve kingdoms (Table 1). The scheme proposed in this paper (Fig. 1, 2, Table 1) is a modification of the Jeffrey (1971) scheme and avoids the taxonomic inflation of the Leedale "fan" scheme which reduces its practical utility. The increase in the number of kingdoms from five in the Jeffrey scheme to seven in the proposed modification results from the treatment of the fungi which are considered to be at least triphyletic. The Oomycora have been removed from the Chromobionta and placed in a separate kingdom, and the myxomycetes have been assigned kingdom status also.

Dillon (1962, 1963) proposed a novel classification based on the comparative cytology and ultrastructure of the cell over a decade ago. He suggested that all living things should be regarded as members of a single kingdom, which he split into fourteen subkingdoms, seven of which included plants. However, Dillon's ideas were promulgated before the recent large accumulation of ultrastructural data and they have not been supported by other workers. He considered the euglenoids and dinoflagellates to be closely related since they possess nonclassical mitosis, but the mitotic mechanism is now known to be fundamentally different in each group (Leedale, 1970). He also included the red algae, the yellow brown algae excluding the dinoflagellates, the fungi, and multicellular animals in a single subkingdom despite differences in pigmentation, thylakoid structure, and flagellation.

The greatest discontinuity between living organisms is that between procaryotes and eucaryotes (Stanier and Van Niel, 1962). The former lack membrane bounded organelles and the complex 9 + 2 strand flagella; their nuclear material is not complexed with histone proteins; they do not have mitotic and meiotic nuclear division. Bold (1973) placed prokaryotic organisms in a subkingdom Prokaryonta, and pigmented eucaryotic organisms and the fungi in the subkingdoms Chloronta

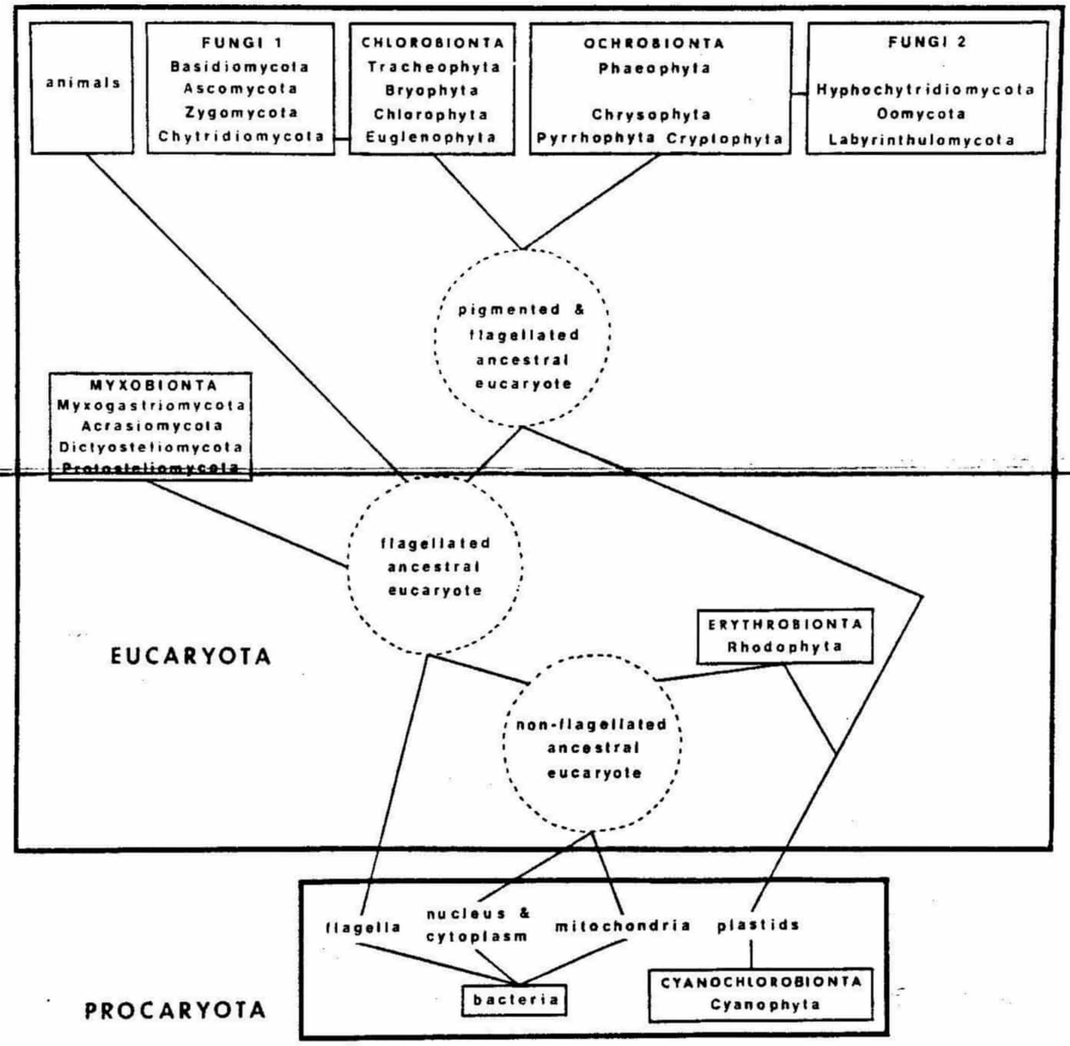

Fig. 2. The endosymbiotic hypothesis for the origin of the eucaryotic cell in which plastids were derived from photosynthetic procaryotes containing chlorophyll *a*, mitochondria from aerobic bacteria, and flagella from spirochaete-like organisms.

and Achloronta, respectively. Neushul (1974) allocated procaryotic organisms to a subkingdom Procaryota and eucaryotic plants to a subkingdom Eucaryota. The latter two authors recognize the kingdom Plantae which implies that they recognize also the two traditional plant and animal kingdoms; thus, perhaps unintentionally, they accord greater significance to this than to the procaryotic – eucaryotic discontinuity. The multiple kingdom systems of Whittaker (1969) and Copeland (1938, 1947, 1956) accord recognition also to the two groups since procaryotic organisms are placed in a distinct kingdom, the Monera. However, greater emphasis would be placed on the two fundamental types of cellular organization if the living world were divided into two groups of equal status as recommended by Lewin (1968), Allsopp (1969), and Klein (1970). Both Jeffrey (1971) and Margulis (1974) divide the living world into two superkingdoms based on the cellular discontinuity. This latter procedure has been followed in the present paper.

There are two hypotheses for the origin of the eucaryotic cell which have a profound influence on the evolution of the various groups within the Eucaryota. The classical view is that lower eucaryotes arose by a process of gradual evolutionary change from photosynthetic procaryotes i.e., the photosynthetic ancestral phytoflagellate, the "uralga", gave rise to the algae and also by loss of autotrophy to the fungi and animals; thus the eucaryotic cell is monophyletic (Fig. 1). The endosymbiotic hypothesis maintains that plastids were derived from Cyanophyta, mitchondria from aerobic bacteria, and flagella from spirochaete – like organisms; thus the eucaryotic cell could have arisen several times i.e., be polyphyletic (Fig. 2). Assuming the validity of the endosymbiosis hypothesis, uncertainty concerning the number of times that the eucaryotic cell may have arisen leads to the discrepancy in the number of kingdoms in the Jeffrey (1971) scheme and the modification proposed in this paper on the one hand, and the Leedale (1974) scheme on the other hand (Table 1). The euglenoids and the green algae are placed in the same kingdom in the former scheme since it is assumed that both taxa evolved subsequently to a single symbiosis between an aerobic bacterium and a photosynthetic procaryote. However, in the latter scheme it is assumed that both groups represent separate evolutionary lines since they were derived by symbioses involving the same photosynthetic procaryote but different aerobic bacteria. The same rationale explains the greater subdivision of the "yellow brown" algae in the Leedale scheme. The endosymbiotic hypothesis has received considerable attention recently (reviews by Sagan, 1967; Margulis, 1970; Taylor, 1974) compared to the classical hypothesis which is supported by Dillon (1962), Allsopp (1969), Klein and Cronquist (1967), Jeffrey (1971), and Uzzell and Spolsky (1974). According to the latter authors "if acceptance in recent scientific literature is a measure of validity, the endosymbiosis hypothesis appears to be almost unchallengeable"; however they present several serious drawbacks to the endosymbiosis hypothesis which should stimulate more bipartite discourse.

Two authors who support the endosymbiosis hypothesis speculated on where the transition from the procaryotic to the eucaryotic condition occurred in plants. Raven (1970) postulated that three groups of photosynthetic procaryotes with different pigment assemblages, the Cyanophyta and two hypothetical groups, the green and yellow procaryotes, appear to be necessary to explain relationships among contemporary organisms; each procaryotic group became involved in an endosymbiosis and subsequently evolved into the plastids of a group of eucaryotic algae. According to Lee (1972), there are serious drawbacks to Raven's hypothesis; there is no evidence that yellow or green procaryotes ever existed and certain cellular structures would be polyphyletic e.g. pyrenoids. However, a procaryotic organism has recently been discovered that lacks phycobilin pigments and has both chlorophylls *a* and *b*, and which may represent the hypothetical green procaryote postulated by Raven (Lewin and Withers, 1975; Lewin, 1975). Lee (1972) postulated a monophyletic origin of plastids from a blue-green alga involved in an endosymbiosis with a colorless member of the Cryptophyta; the remainder of the eucaryotic algae subsequently evolved along three independent lines: (i) to

the Chlorophyta by loss of phycobilins and the acquisition of chlorophyll *b* (ii) the evolution of chlorophyll *c* and then a split, to the plastids of the Cryptophyta and to the rest of chlorophyll *c* bearing algae by loss of phycobilins and (iii) by loss of flagella to the Rhodophyta. A weakness in this scheme is that the Rhodophyta are probably more closely related in several respects to the Cyanophyta than they are to other eucaryotes, i.e., there is no evidence that the Rhodophyta ever possessed flagella (Klein, 1970; Pickett-Heaps, 1974) and their phycobilin pigments are immunologically related to those of the Cyanophyta but are apparently distinct from those of the Cryptophyta (Berns, 1967; Glazer, Cohen-Bazire and Stanier, 1971). Thus the Rhodophyta are probably relatively primitive eucaryotic algae and were not derived from flagellated eucaryotic algae.

Comparative biochemistry has demonstrated the underlying uniformity of many metabolic processes, the "unity of biochemistry," in living organisms; it is of major importance in providing clues of phylogenetic relationships in organisms which do not fossilize (Aaronson and Hutner, 1966). Pigment composition, especially the chlorophylls, may be such a feature, a phylogenetically conservative character (Lewin, 1974).

Chlorophyll *a* is a conservative and primitive character state since it occurs in all photosynthetic plants from procaryotic blue-green algae to seed plants. Its presence in all aerobic photosynthetic plants indicates that they had a common origin (Strain, 1955). The remaining three chlorophylls, *b*, *c*, and *d* are derived or specialized character states since they have a more restricted distribution, and are probably reliable phylogenetic markers. Dougherty (1955), Strain (1955), and Silva (1956) suggested the possible taxonomic significance of the distribution of the various kinds of chlorophyll, but Christensen in 1962 (review in Round, 1963) was the first to use the distribution of chlorophylls in a formal scheme to group algal classes in higher taxonomic assemblages. Christensen based his classification on the presence or absence of nuclei and flagella and on the type of chlorophylls, and arranged the eucaryotic algae in three remotely-related groups. He assumed that nuclei, flagella, and chlorophylls *b* and *c* arose only once in evolution and in that sequence. The Procaryota contained the Cyanophyta, and the Eucaryota was divided into two groups, the Aconta without motile cells containing the Rhodophyta, and the Contophora for algae with motile cells; the latter group contained the Chlorophyta possessing chlorophyll *b* and the Chromophyta with chlorophyll *c*. In a subsequent publication however, he relinquished the names of the higher taxa (Christensen, 1964). It is proposed that the distribution of accessory chlorophyll as suggested by Christensen be used as a major taxonomic criterion for the classification of photosynthetic plants at the kingdom level in the superkingdom Eucaryota (Fig. 1, 2). The kingdom Cyanochlorobionta within the superkingdom Procaryota contains the single division Cyanophyta with no accessory chlorophyll (blue-green plant line). Within the superkingdom Eucaryota the kingdom Erythrobionta with the single division Rhodophyta has no accessory chlorophyll or occasionally chlorophyll *d* (red plant line), the kingdom Chlorobionta with the divisions Chlorophyta, Euglenophyta, Bryophyta and Tracheophyta has accessory chlorophyll *b* (green plant line), and the kingdom Ochrobionta with the divisions Chrysophyta, Cryptophyta, Phaeophyta and Pyrrhophyta has accessory chlorophyl *c* (yellow-brown plant line); although two algae within the class Eustigmatophyceae, division Chrysophyta, may have no accessory chlorophyll, its absence is probably due to loss since on other grounds these algae do not appear to be primitive (Meeks, 1974). Strain (1955) reported traces of a fifth chlorophyll, *e*, in the chrysophyte *Tribonema bombycinum* but this is now thought to be an alteration of chlorophyll *c* due to methanol extraction (Meeks, 1974). Thus, terrestrial plants have been formally included in the same taxon as the Chlorophyta. Smith (1950) suggested that the major groups of algae be regarded as kingdoms and that the "kingdom of the grass-green plants" consists of green algae, the bryophytes, the pteridophytes and the higher plants. Jeffrey (1971) and Leedale (1974) both include terrestrial plants in the same kingdom as the green algae. Doyle (1970) and Fott (1974) also allocated all

green plants to a single taxon, the division Chlorophyta, but their scheme is unlikely to gain widespread acceptance since it creates a group of unwiedly proportions. The names of the subkingdoms have been derived from the Greek word *bion*, the present participle of *bioun*, to live, and from the Greek words for color: *cyanos*, blue; *chloros*, green; *erythros*, red; *ochros*, yellow-brown. The name Ochrobionta has been coined to replace the Chromophyta (Greek *chroma*, color) of Christensen since the former is more descriptive and conforms to the derivation of the names of the other three subkingdoms from the predominant color of the organisms in the group.

Various cytological and biochemical criteria tend to support the circumscription of the subkingdoms based on chlorophyll distribution, but no other single character alone may be used to adequately define these taxa e.g., ultrastructure (Bourrelly, 1961; Dodge, 1973; Manton, 1965), carotenoids (Bisalputra, 1974; Goodwin, 1974), reserve food products (Craigie, 1974); cell wall chemistry (Mackie and Preston, 1974); and mitosis (Leedale, 1970; Pickett-Heaps, 1972, 1974). Chaudefaud (1950) established the group Chromophycées (changed to Chromophycophytes in 1960) on ultrastructural criteria but with the exception of the Euglenophyta his taxon is more or less identical to the Ochrobionta based on the distribution of chlorophyll *c*.

The Ochrobionta contains algae which are usually yellowish-brown to brown in color due to a preponderance of carotenoids over chlorophylls; however the Xanthophyceae in the Chrysophyta are generally green in color and the Cryptophyta vary in color from brown to green, red, blue, or blue-green (Butcher, 1967). Since the phycocyanin and phycoerythrin of the Cryptophyta are immunologically unrelated to those present in the Cyanophyta and Rhodophyta which are immunologically similar to each other (Berns, 1967; Glazer, Cohen-Bazire, and Stanier 1971) the presence of these pigments in the Cryptophyta probably represents a separate evolutionary development i.e., phycobilins appear to be diphyletic. Since phycobilins may be by-products of chlorophyll biosynthesis (Allen, Dougherty and McLaughlin, 1959), the potential to produce these pigments is probably inherent in all algae. The Euglenophyta in the Chlorobionta and the Cryptophyta and Pyrrhophyta in the Ochrobionta have several ultrastructural features in common (Dodge, 1973; Lee, 1972); these divisions are placed at the base of their respective kingdoms to indicate that these groups possibly did not evolve far in certain cellular features after the evolution of accessory chlorophylls (Figs. 1, 2).

The Pyrrhophyta have been assigned by Dodge (1965) to a new kingdom, the Mesokaryota, based on their nuclear organization which is held to be intermediate between that of procaryotes and eucaryotes; the chromosomes remain condensed throughout the mitotic cycle and like those of bacteria were thought to lack proteins of any kind (Dodge, 1966, 1973). However, recent findings suggest that the significance of the mesocaryotic nucleus in dinoflagellates may not be as profound as previously thought; a study with immunofluorescent techniques has indicated that a complex of histone – DNA may be present in the chromosomes of dinoflagellates (Stewart and Beck, 1967); two dinoflagellate chromatins contain protein although most is not soluble in acid as are histones, and the small amount of acid-soluble protein did not give the characteristic histone banding pattern on polyacrylamide gel electrophoresis; members of the division Euglenophyta have highly condensed chromosomes in the interphase nucleus (Dodge, 1973); one dinoflagellate has a mesocaryotic and a eucaryotic nucleus within the same cell (Dodge, 1973). In *Peridinium balticum*, which has both a mesocaryotic and a eucaryotic nucleus, the latter may be of foreign origin. A single membrane surrounds the eucaryotic nucleus and the chloroplasts and isolates them from the rest of the cytoplasm indicating that there may be a symbiotic relationship between a photosynthetic endosymbiont and the dinoflagellate cytoplasm (Tomas, Cox and Steidinger, 1973; Tomas and Cox, 1973). Zingmark (1970) however, presents evidence that the two kinds of nuclei in *Noctiluca* are found in different phases of the life history and are thus ontogenetically related.

The Erythrobionta contains the Rhodophyta in which flagellated cells are absent. Lee (1970) and Margulis (1974) suggested that the group may have been derived from a flagellated ancestor; however, there is no evidence to support this contention and the view is maintained here that the red algae probably originated from the eucaryotic cell prior to the acquisition of the centriole – basal body apparatus (Klein and Cronquist, 1967; Klein, 1970; Pickett-Heaps, 1974).

There is no general agreement on the delimitation of vascular plants into divisions; in the eighteen books examined, seven authors recognize a single division, the Tracheophyta, but the remainder split them into seven to eleven divisions. The vascular plants have been placed in the Tracheophyta in the proposed scheme since they are all biochemically similar (chlorophylls *a* and *b*, similar carotenoids, starch as a reserve food product) and they have morphological similarities in terms of the presence of vascular tissue containing xylem and phloem, and a life history consisting of an alternation of generations. This also has the advantage of bringing the classification of vascular plants into line with the more stable zoological system; the higher animals, although as diverse when mature as tunicates and humans, are all placed in the phylum Chordata because of the presence of a notochord, pharyngeal gill slits, and a hollow, dorsal nerve cord in the embryo. This is an important consideration if a single, universal, classificatory scheme of living organisms is ever to be devised.

Numerous hypotheses for the origin of the fungi have been proposed; some seek to derive the fungi from the Protozoa but most consider that they have evolved from the algae because of morphological similarities such as the presence of cell walls, antheridia and oogonia in the Oomycota, and flagellated cells in many lower fungi (Martin, 1955, 1968; Cain, 1972; Bessey, 1942). Recently there has been a revival of the hypothesis of an evolutionary link between the Rhodophyta and the Ascomycota (Demoulin, 1974; Kohlmeyer, 1975); the latter author has described a new order of marine fungi, the Spathulosporales, with many primitive features, parasitic on red algae, which he considers provides additional evidence for the purported link. Chadefaud (1975) has recently propounded a "para-floridean" hypothesis for the origin of the Ascomycota, which supposes that the Rhodophyta and Ascomycota underwent parallel evolution from a common ancestor derived from the point from which the Rhodophyta evolved from the Cyanophyta. However, the algal-fungus morphological similarities could be due to morphological convergence (Saville, 1968; Dixon, 1973) and biochemical data should be sought before further speculation.

Recent ultrastructural and biochemical data indicate a possible derivation of the lower fungi from the algae, and the subsequent evolution of the Ascomycota and the Basidiomycota. A second centriole is present in certain members of both the Chytridiomycota, with a single posterior whiplash flagellum (Koch, 1968), and the Hyphochytridiomycota, with a single anterior tinsel flagellum (Renaud and Swift, 1964); this suggests and origin from biflagellated organisms or from organisms with biflagellated cells. Hutchinson (1967), Jeffrey (1971), and Leedale (1974) classified the Oomycota with those algae placed in the Ochrobionta in the proposed scheme due to a similarity in flagellated cells, but they have been assigned, with the Hypochytridiomycota, to a separate kingdom in the proposed scheme. Cellulose has been detected in the cell walls of several fungi although important cell wall polymers of some fungi, e.g., chitin, have not been found in the algae (Parker, Preston and Fogg, 1963; Bartnicki-Garcia, 1971; Jewell, 1974). Two distinct pathways for the synthesis of lysine occur in the fungi and since each pathway involves numerous enzymes it seems improbable that they could have evolved sporadically. The $\alpha - \varepsilon$ – diaminopimelic acid (DAP) pathway occurs in the Oomycota and the Hyphochytridiomycota and also in bacteria, blue-green algae, mosses, liverworts, ferns, gymnosperms and angiosperms; the α – aminoadipic acid (AAA) pathway is present in the Chytridiomycota, Zygomycota, Ascomycota and Basidiomycota and also in the euglenoid flagellates. The DAP lysine pathway evolved before the AAA lysine pathway since the former occurs in both procaryotes and eucaryotes, whereas the latter is found only in eucaryotes.

It is thought that an irreversible loss of the DAP lysine pathway preceeded the evolution of the AAA lysine pathway (Vogel et al., 1970). These data suggest that the fungi may have evolved from disparate algal groups, the Euglenophyta, and possibly the Chlorophyta although the flagellation of the lower fungi with the DAP lysine pathway suggests that the Chrysophyta may be more likely progenitors. Data on lysine synthesis of members from the latter division may help to elucidate the possible evolutionary pathway. The data indicate the possibility of the evolution of the higher fungi from the Chytridiomycota, a view which ultrastructural observations on septa and special membranes in these two groups also supports (Moore, 1971). However, lysine pathway data from members of the Rhodophyta would provide needed biochemical information that would test the hypothesis of the derivation of the Ascomycota by way of this algal division.

The kingdom Myxobionta includes the plasmodial slime molds and the cellular slime molds. Many authors regard them as Protozoa because a cell wall is absent in the trophic stage and nutrition is primarily holozoic. However, here they are regarded as plants because many have plant like fruiting bodies containing spores which in some species have cellulose cell walls (Olive, 1970). Olive (1970) has recently described a new group of relatively simple slime molds, the protostelids, from which he believes both the plasmodial and cellular slime molds were derived. Olive (1970) subdivided the slime molds into four subclasses which have been raised to divisional status in the proposed classification.

The labyrinthulids, the net slime molds, are probably not related to the other slime molds (Olive, 1970). Since they have laterally biflagellated (anterior tinsel and posterior whiplash) pyriform zoospores with a stigma (Amon and Perkins, 1968), they may have been derived from the Ochrobionta and thus have been assigned tentatively to the same kingdom as the Oomycota and the Hyphochytridiomycota.

The information obtained to date indicates that the fungi are at least triphyletic and with the exception of the Myxobionta may have been derived from algae from two kingdoms, the Chlorobionta and the Ochrobionta, and possibly even from the Erythrobionta.

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TABLE 1 – Monophyletic Kingdom Classificatory Schemes

Leedale (1974)	*Jeffrey (1971)*	*Edwards*
Monera	*Cyanobionta*	*Cyanochlorobionta*
Cyanophyta	Cyanophyta	Cyanophyta
Red Algae	*Rhodobionta*	*Erythrobionta*
Rhodophyta	Rhodophyta	Rhodophyta
Plantae	*Chlorobionta*	*Chlorobionta*
Chlorophyta	Chlorophyta	Chlorophyta
	Zygophyta	
	Loxophyta	
	Prasinophyta	
Charophyta	Streptophyta	
Bryophyta		Bryophyta
Tracheophyta		Tracheophyta
Euglenoids		
Euglenophyta	Euglenophyta	Euglenophyta
Myxomycetes	*Mycobionta*	*Myxobionta*
Myxomycota	(not subdivided)	Myxogastriomycota
		Dictyosteliomycota
		Acrasiomycota
		Protosteliomycota
Fungi		*Fungi 1*
Zygomycota		Zygomycota
Ascomycota		Ascomycota
Basidiomycota		Basidiomycota
Chytrids		
Chytridiomycota		Chytridiomycota
		Fungi 2
		Labyrinthulomycota
		Hyphochytridiomycota
Heterokonts	*Chromobionta*	
Oomycota	Oomycota	Oomycota
		Ochrobionta
Phaeophyta	Phaeophyta	Phaeophyta
Chrysophyta	Chrysophyta	Chrysophyta
	Chloromonadophyta	
Bacillariophyta	Bacillariophyta	
Xanthophyta	Xanthophyta	
Eustigs		
Eustigmatophyta		
Haptophytes		
Haptophyta	Haptophyta	
Cryptomonads		
Cryptophyta	Cryptophyta	Cryptophyta
Dinoflagellates		
Dinophyta	Dinophyta	Pyrrhophyta